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Energy Requirements for Molt in the Kestrel *Falco tinnunculus*

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Abstract

*We estimated energy requirements for plumage replacement in the kestrel (*Falco tinnunculus*) by comparing O_2 consumption $\dot{V}O_2$ and metabolizable energy intake during molt and nonmolt. The energy expenditure for feather synthesis (*S*) as derived from the regression of basal metabolic rate (BMR) on molt intensity was 104 kJ· (g dry feathers)$^{-1}$. As derived from the regression of the resting metabolic rate of nonfasting birds at night (RMR) on molt intensity,* S *was 108 kJ· g^{-1}, and statistically indistinguishable from the BMR estimate. During the first part of molt the coefficient of temperature dependence of the standard metabolic rate below thermoneutrality (SMR) increased from 0.050 to 0.070 W· °C^{-1}. The metabolizable energy required for maintenance (M_m) increased with increasing body mass. The M_m in males was higher than in females of the same body mass. The M_m during molt was higher than during nonmolt episodes. The estimate for the cost of feather synthesis based on this difference was* S = 117 kJ· g^{-1}. *The cost of feather synthesis in the kestrel is thus much lower than values reported for three passerines (230–835 kJ· g^{-1}). This difference in efficiency may be related to diet (carnivorous vs. granivorous birds) or body mass.*

Introduction

Avian molt has a major impact on the daily balance of energy. Molt thereby potentially competes in the annual cycle with other vital functions, and in

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most species molt, reproduction, and migration are temporally nonoverlapping phases (Murton and Westwood 1977, fig. 7.5). Assessments of the energy costs of molt have been made only in a few passerine birds (Blackmore 1969; Dolnik and Gavrilov 1979; J. D. Chilgren, quoted in King 1981; Murphy and King 1984*a*). In the framework of a study on the seasonal variations in the components of the daily energy budget in the European kestrel (Masman 1986; Masman, Daan, and Dijkstra 1986*a;* Masman et al. 1986*b;* Masman and Klaassen 1987; Masman, Daan, and Beldhuis 1988), we have measured the energy costs associated with molt.

There are two major components of the energy costs associated with molt (King 1981): (1) the energy required for the production of new feathers and (2) the energy required to offset heat loss resulting from the decrease of insulation during molt. The increment due to increased conductance can be evaluated by indirect calorimetry at subthermoneutral temperatures. The cost of feather synthesis can be assessed in two ways, by measuring the increased metabolizable energy intake ($\dot{M}$) or by measuring the increased O_2 consumption ($\dot{V}O_2$) during molt (Blackmore 1969; Dolnik and Gavrilov 1979; King 1981). The first method is based on the assumption that increased energy intake compensates for feather synthesis costs and not for a limited presence in the food of specific critical nutrients. The proposition that the increased food intake reflects a need for critical amino acids has indeed been discounted (Gavrilov and Dolnik 1974; Dolnik and Gavrilov 1979; Murphy and King 1984*a*). A further assumption in the procedure is that the energy expenditure for activity is the same during control and molt periods. This condition is not always met (King 1981), and variations in activity influence the accuracy of the method. An advantage of the method is that the overall increase in energetic demands during molt is measured. The energy for feather synthesis, the energy content of the feathers replaced, and possible circadian variations in molt intensity (R) are taken into account.

The second method compares the basal metabolic rate (BMR) of molting and nonmolting birds. The increase in BMR is interpreted as the energy expenditure for feather synthesis (S). Energy expenditure for locomotion can be assumed to be constant (i.e., minimal) over the molt and control measurements. However, feather synthesis during nocturnal postabsorptive rest may not be representative of the 24-h rate of synthesis (see Walsberg 1983), and fasting per se may interfere with the progress of molt.

We base our estimates of S on both $\dot{V}O_2$ (fasting and nonfasting), and daily $\dot{M}$ during molt and nonmolt periods. In addition, we have measured the effect of molt on the increase in metabolic rate with reduced ambient temperatures (T_a's) by indirect calorimetry.

Material and Methods

Animals and Housing

Kestrels (*Falco tinnunculus*) were caught by *bal-chatri* (Cavé 1968) near Lauwersmeer, The Netherlands (53°20′N, 6°12′E). They were trained to fly indoors (Masman and Klaassen 1987) and to sit quietly, tethered on a perch (Glasier 1978). The birds were usually exercised daily, for up to 2 h, from 1 wk after capture until the experiments started. The birds were housed under the natural seasonal L:D cycle at a T_a of 15°–20°C. They were fed ad lib. once per day (ca 1600 hours) with eviscerated laboratory mice 6 d per week and day-old cockerels once per week, supplemented with a calcium-vitamin mixture (Carnicon®). We weighed the food offered (to 0.1 g) and the leftovers from the previous day. Mass of the leftovers was corrected for dehydration loss. Daily M was calculated for days of mouse feeding from an energy content of 7.8 kJ · g^{-1} fresh mouse and an assimilation quotient of 0.78 (Masman et al. 1986*b*, table 5). Kestrels were weighed to 0.1 g each day prior to feeding. During molt all feathers shed were collected daily. Body feather molt was recorded once a week on five feather fields (head + nape; back; rump + upper tail coverts; breast, belly flanks + under tail coverts; wing coverts) by scoring the fractions of feathers missing, feathers growing, and feathers renewed completely. Molt of the flight feathers was described by measuring the length of each growing feather to 1 mm once per week.

Indirect Calorimetry

Metabolic heat production was calculated from $\dot{V}O_2$ and CO_2 production ($\dot{V}CO_2$) in an open-flow system. The birds sat on a perch in a 24-L metabolic chamber at a flow rate of 120–160 L · h^{-1} (calibrated oil flowmeter). Oxygen concentrations were measured with a zirconium oxide analyzer (Ametek S3A), and CO_2 concentrations with an infrared beam CO_2 analyzer (Binos, Leybold Heraeus). All outputs were recorded on a Philips PR 4010/00 chart recorder. Volumes were corrected to STPD and for composition changes due to RQ values lower than one (Hill 1972). On the basis of 397 runs of parallel $\dot{V}CO_2$ and $\dot{V}O_2$ records we obtained a mean respiratory quotient of 0.769 (SE = 0.001). Together with the composition of the kestrel food (fractions of ash-free dry mass: fat = 0.293; protein = 0.707), this value leads to an energy equivalence of O_2 of 19.5 kJ · L^{-1} (Masman and Klaassen 1987).

Body mass (W) varied with season in individuals. In order to eliminate W effects on energy expenditure, we first expressed metabolic rates on a mass-specific basis. This is based on the finding that intraindividual variation

in BMR is nearly proportional to W in the kestrel (Daan et al. 1989). To be able to arrive at a measure of molt costs we then transformed mass-specific data back to whole-animal metabolism by multiplication with the average individual mass.

Molt Intensity

To quantify R, we expressed molt as the fraction of total feather quantity replaced per week for each individual on the basis of the molt scores. Total mass of the different feather categories was measured by plucking four (two male, two female) dead kestrels. Two of these (one male, one female) had died in November/December (after molt), the other two in April/May (before molt). Relative feather mass of the winter birds (11.8%) did not exceed that of the spring birds (12.5%). Hence, we could not correct for potential feather wear. We expressed R in grams of dry feathers produced per day by multiplying the fraction of feathers replaced with the total mass for each of the feather categories.

Experimental Design

From May 1984 until June 1985 two series of measurements were carried out on four kestrels, one of each sex per series.

Series I. On alternate weeks during 1 yr we recorded $\dot{V}O_2$ continuously in two birds for 72 h and $\dot{V}CO_2$ in one of these birds. A known mass of laboratory mice was offered inside the chamber at the beginning of each run (ca. 1600 hours). After 24 h the birds were weighed again and returned to the chamber without food. After 48 h the birds were weighed once more and again mice were offered in the chamber. The T_a in the metabolic chamber was maintained at 21° ± 0.5°C (thermoneutral, see fig. 7), and the L:D cycle was adjusted to the current natural day length. On the basis of Series I we describe seasonal variation in (1) BMR, defined as the lowest nocturnal $\dot{V}O_2$ in darkness under fasting and resting conditions at thermoneutrality (night 2), and (2) in RMR, under conditions identical to those used for BMR except that food is being digested (nights 1 and 3). The differences in $\dot{V}O_2$'s between night 2 and nights 1 and 3 reflect the heat increment of feeding (H) and have been reported on elsewhere (Masman, Daan, and Dietz 1989).

Series II. We measured the $\dot{V}O_2$ of one male and one female kestrel at various T_a's during the night (on a 48-h feeding schedule) under fasting and fed

conditions over the course of 1 yr, once per month for six successive nights. The $\dot{V}CO_2$ was recorded for one of the two birds. The lowest $\dot{V}O_2$ at each temperature on the uneven nights (fasting) was taken as the SMR. Test temperatures were 30° and 20°C (about 6 h each night) on nights 1 and 2; 12° and 8°C on nights 3 and 4; and −15° and −3°C on nights 5 and 6. We fitted equations of the form

$$\dot{V}O_2 = a + b \cdot T_a \quad \text{for } T_a < T_{lc} \text{ (SMR)} \tag{1}$$

and

$$\dot{V}O_2 = c \qquad \text{for } T_a > T_{lc} \text{ (BMR)} \tag{2}$$

(for T_a in °C; T_{lc} is the lower critical temperature in °C) to the data. This was done by the "hockey stick routine" (H. Beldhuis, personal communication), generating least squares approximations to both equations for any combination of data points contributing to the regression and the flat part of the model and then selecting the solution with the smallest total sum of squares. The T_{lc} is then estimated by $T_{lc} = (c-a)/b$ °C. We did not measure body temperature throughout the annual cycle; hence, we cannot formally compute thermal conductance (McNab 1980). However, the temperature coefficient b in different phases is an index of the rate of heat loss at subthermoneutral temperatures.

Series II was used to describe the seasonal variations in BMR, T_{lc} and b. When the birds were not involved in the measurements of Series I or II, daily M and body mass change (δW) were monitored. These records were used to describe (1) the mass-specific energy requirement for maintenance (M_m) during molting and nonmolting periods, and (2) the metabolizable energy expended or gained by changing W, that is, the cost of body tissue deposition.

Results

Feather Synthesis

Indirect Calorimetry. Body mass varied considerably in the course of the year, in spite of ad lib. feeding throughout (fig. 1*a*). Body mass was lowest around the beginning of molt. During molt, BMR was elevated relative to the nonmolting periods (fig. 1*b*), which reflects S.

Total molt duration was on average 180 d, while flight feather replacement lasted about 130 d (fig. 2). Timing and duration of molt in captive kestrels

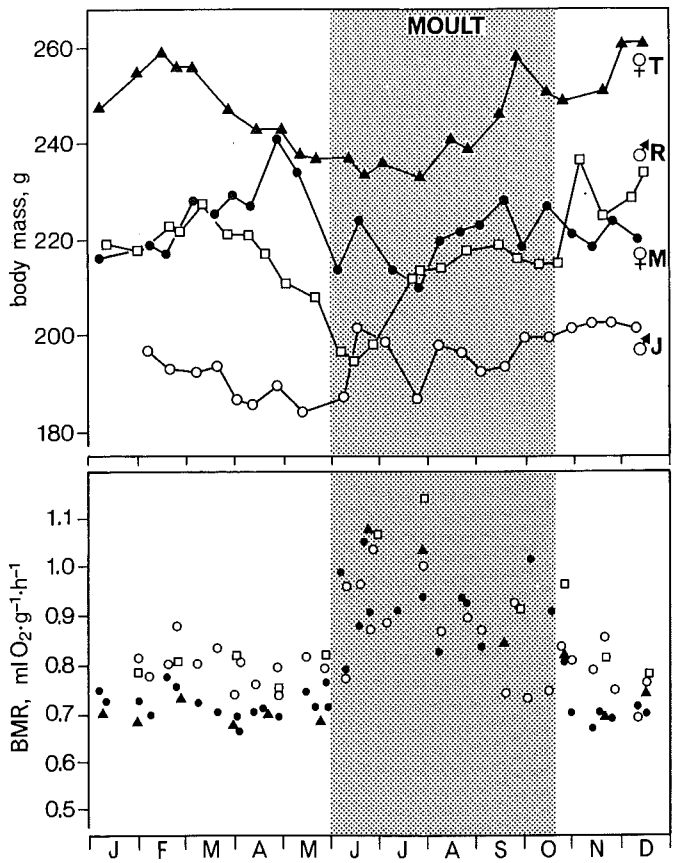

Fig. 1. Seasonal variation in W *(top) and BMR (bottom) for four individual kestrels. Indicated is* W *as measured prior to each experiment of Series I and II. The gray bar indicates the average molting period for the four birds.*

corresponded to that of kestrels in the field (Masman 1986). To express the weekly molt data in grams of feathers produced we used the feather weights of four birds dissected, which are presented in table 1. The average R was highest for both sexes between 40 and 120 d after molt onset (0.156 $g \cdot d^{-1}$ in males; 0.216 $g \cdot d^{-1}$ in females; see fig. 3). For each experiment of Series I and II we related the R of each individual to its $\dot{V}O_2$. Mass-specific BMR increased with increased R (fig. 4). After transformation to whole-bird metabolism by multiplication of each BMR measurement with the average individual mass, we performed a MANOVA. The interaction term sex × R did not contribute significantly to the explained variance ($F_{1,88} = 1.18$, $P > 0.05$). Hence, we assumed equal slopes for males and females and found significant

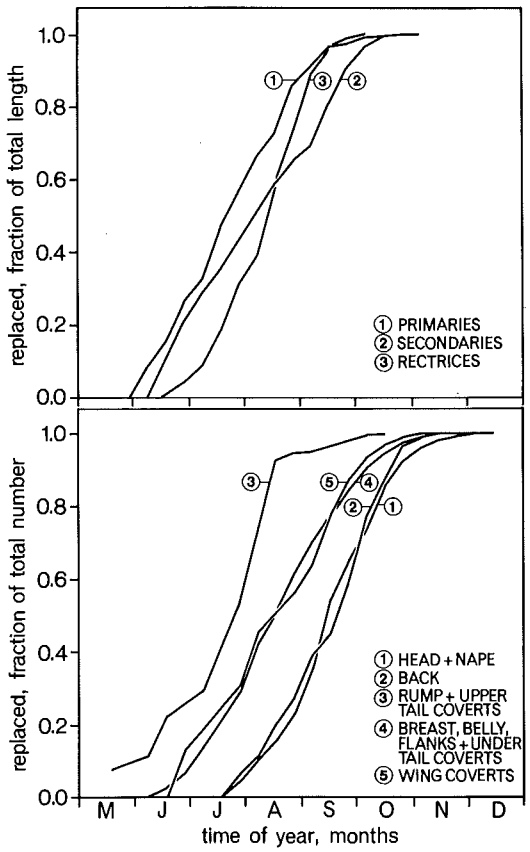

Fig. 2. Average molt rate of flight feathers, expressed as a fraction of total flight feather length, and of body feathers, expressed as a fraction of the total number that have been replaced as a function of time.

contributions of both R and sex (R: $F_{1,89} = 70.65$, $P < 0.001$; sex: $F_{1,89} = 6.70$, $P < 0.05$). The relationships are then best described by the regressions

$$\text{BMR} = 156.45 + 5.33 \cdot R \text{ mL } O_2 \cdot h^{-1} \quad \text{for males} \tag{3}$$

and

$$\text{BMR} = 165.91 + 5.33 \cdot R \text{ mL } O_2 \cdot h^{-1} \quad \text{for females,} \tag{4}$$

where R is the dry feather production rate in $mg \cdot h^{-1}$. The slope of the regressions, when multiplied by the energetic equivalent of 19.5 $J \cdot (mL\ O_2)^{-1}$, yields the estimate of S, the energy expenditure for feather synthesis excluding the energy content of the feathers formed: $S = 104$ $kJ \cdot (g \cdot \text{dry feather})^{-1}$.

TABLE 1
Dry mass (g) of flight and body feathers of four nonmolting kestrels

	Female	Female	Male	Male
Primaries	3.59	3.64	3.51	2.93
Secondaries	1.67	1.58	1.58	1.33
Rectrices	2.39	2.18	2.28	1.84
Body feathers ...	17.50	13.46	11.07	9.67
Total	25.15	20.86	18.44	15.86

Since BMR is measured in postabsorptive resting birds the question arises whether molt in this condition is representative also of molt in nonfasting birds. Therefore, RMR was also regressed on R. Because RMR gradually decreases after a meal (Masman et al. 1989), we used only RMR values obtained between 8 and 12 h after a meal of 18.5 g lab mouse. Mass-specific RMR again increased with R (not shown). After transformation to whole-bird metabolism we again performed a MANOVA. The interaction term sex $\times$ R did not contribute significantly to the explained variance ($F_{1,92} = 1.04$, $P > 0.05$). Hence, we assumed equal slopes for males and females and found significant contributions of both R and sex (R: $F_{1,93} = 55.83$, $P < 0.001$; sex: $F_{1,93} = 7.96$, $P < 0.01$). The relationships are then best described by the regressions

$$\text{RMR} = 204.56 + 5.52 \cdot R \text{ mL } O_2 \cdot h^{-1} \quad \text{for males} \tag{5}$$

and

$$\text{RMR} = 217.64 + 5.52 \cdot R \text{ mL } O_2 \cdot h^{-1} \quad \text{for females.} \tag{6}$$

The slope of 5.52 yields an estimate for S of 108 kJ $\cdot$ (g $\cdot$ dry feather)$^{-1}$. In a MANOVA on all measurements, the interaction term type (BMR or RMR) $\times$ R $\times$ sex did not significantly contribute to the explained variance ($F_{1,183} = 0.50$, $P > 0.05$). After assuming a common slope, type, sex, and molt did contribute significantly to the explained variance. Thus, the estimates for S based on BMR and RMR were not significantly different, but RMR was on average 50.4 mL $O_2 \cdot h^{-1}$ above BMR. Our final estimate of S based on BMR and RMR in males and females is this: $S = 106$ kJ $\cdot$ (g $\cdot$ dry feather)$^{-1}$.

The total energy expenditure for feather replacement (S') is estimated by adding the energy content of kestrel feathers (D) to the cost of feather synthesis (S). This D was measured by E. Keijer in our laboratory on kestrel

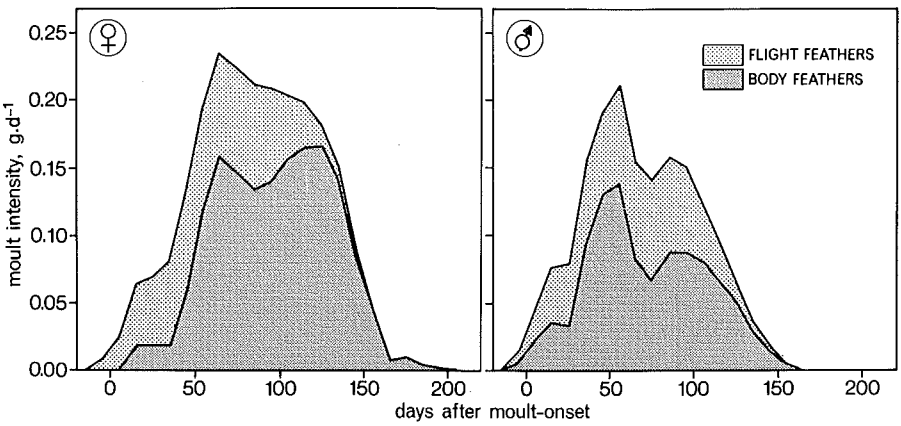

Fig. 3. Average R *(dry feathers replaced in* $g \cdot d^{-1}$*) as a function of time relative to molt onset.*

feathers from two birds and equaled 23.4 $kJ \cdot g^{-1}$, in close agreement with values reported for other birds (22 $kJ \cdot g^{-1}$; Murphy and King 1982). Thus, $S' = S + D = 129\ kJ \cdot g^{-1}$.

Metabolizable Energy Intake. Energy requirements for plumage replacement were independently estimated by a comparison of daily M during molt and nonmolt episodes. Because M_m varies with W, we corrected for seasonal variations in W. An example of the relationship between daily net energy intake and δW is shown in figure 5. We analyzed the relationship between daily δW and M in different classes of W separately. The intercept at $\delta W = 0$ in the linear regression of δW on M yields an estimate for M_m at a given mass maintained.

All available data on daily M and δW, for days on which the food consisted of lab mice (619 bird-days), were pooled per individual for six categories of maintained W for molt and nonmolt periods separately (see table 2). Energy for maintenance in males was greater than female M_m (fig. 6), which confirms the apparent physiological difference between males and females described for BMR (Daan et al. 1989). Energy for maintenance was further elevated during molt in both sexes. This elevation can be interpreted as the extra energy expenditure for feather replacement (S'). Over all days in the molting period M_m was significantly elevated during molt by 17.8 $kJ \cdot d^{-1}$ in males and by 16.7 $kJ \cdot d^{-1}$ in females (MANOVA; in both sexes the interaction molt × mass was not significant, whereas molt was significant: for females, $F_{7,1} = 14.1$, $P < 0.01$; for males, $F_{5,1} = 13.7$; $P < 0.02$). The average S' was 0.11 $g \cdot d^{-1}$ in males and 0.14 $g \cdot d^{-1}$ in females. The mean S' is thus estimated

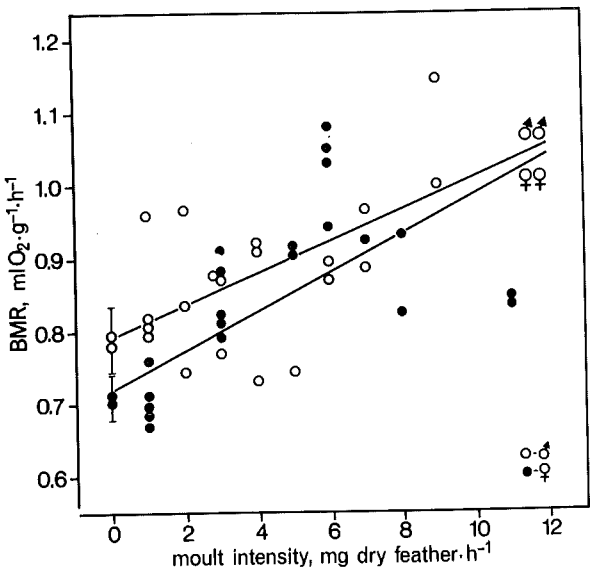

Fig. 4. Mass-specific BMR as a function of R *for males (open circles) and females (solid circles). Each circle indicates one experiment in Series I or II during molt. Lines show regressions for males and females separately. For the nonmolting period, data were pooled per individual (±SD, vertical bars).*

by $S' = 17.8/0.11 = 162$ kJ · g^{-1} in males and $S' = 16.7/0.14 = 119$ kJ · g^{-1} in females, or on average 140 kJ · g^{-1}. These estimates are on the same order as the estimate from indirect calorimetry (129 kJ · g^{-1}). Subtraction of D (23.4 kJ · g^{-1}) gives a second estimate of the costs of feather synthesis: $S = 117$ kJ · g^{-1}.

There was no evidence for a difference in the relationship between M and δW, above and below the maintenance point (fig. 5; see also Kirkwood 1981). Therefore, the slope of the regression lines can be used as an estimate (ε, kJ · g^{-1}) of the metabolic energy involved in body tissue deposition. Within individuals and between individuals of the same sex and the same phase (molt vs. nonmolt) M_m increased with increasing W. The estimate ε did not vary systematically with mass and was on average 19.2 kJ · g^{-1} (SD = 6.5, $n = 18$; table 2).

Temperature Coefficient of Standard Metabolic Rate

During the first part of molt (June–August) there was a sharp increase in fasting heat loss at low temperatures (fig. 7). However, T_{lc} only slightly

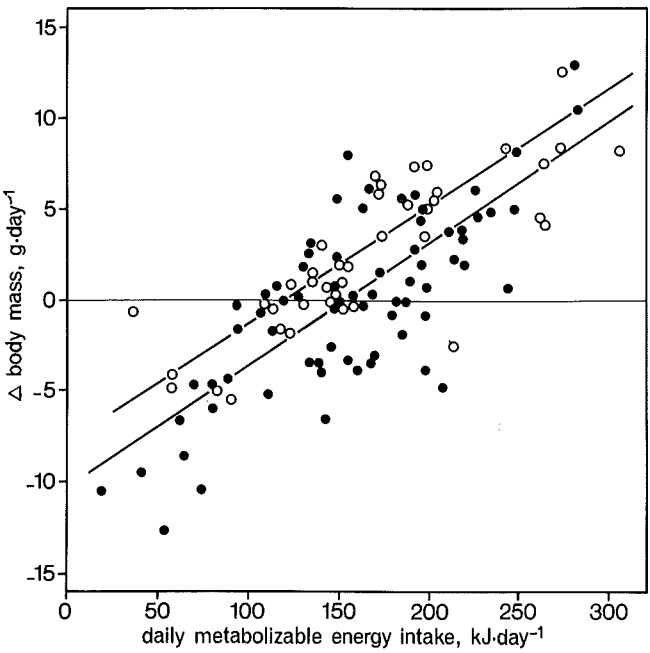

Fig. 5. Daily δW *as a function of daily* M *for female M in the nonmolting period maintaining spontaneously different* W*'s. Two situations are indicated, days on which* W *before feeding was 205–220 g (open circles) and days on which* W *was 220–235 g (solid circles). Lines were calculated by linear regression (see table 2).*

increased during the first part of molt (ca. 1°C; table 3). During winter (November–March) the temperature coefficient *b* was rather stable around 0.04 mL $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$ (table 3), or 0.2 $W \cdot kg^{-1} \cdot °C^{-1}$ (fig. 8) in both sexes. The temperature coefficient increased just before the onset of molt and reached a maximum in the first 2 mo of molt (fig. 8).

Discussion

The energetic cost of feather synthesis in the kestrel obtained here (106 $kJ \cdot g^{-1}$ by indirect calorimetry, 117 $kJ \cdot g^{-1}$ by maintenance metabolism) is much lower than the values reported for three passerines (230–835 $kJ \cdot g^{-1}$; table 4). Wijnandts (1984) reported an increase in BMR related to flight feather molt in the long-eared owl, *Asio otus,* and established a regression of BMR on flight feather *R* with a slope of 0.0052 mL $O_2 \cdot min^{-1} \cdot kg^{-1}/(mg$

TABLE 2
Estimates of daily M_m *and* ε

Mass (in grams) and Bird	Molt M_m (kJ · d^{-1})	Molt ε (kJ · g^{-1})	Molt n	Nonmolt M_m (kJ · d^{-1})	Nonmolt ε (kJ · g^{-1})	Nonmolt n
175–190:						
Male J	161.0	10.8	10	135.1	27.0	36
190–205:						
Male J	174.3	18.9	56	166.7	22.2	60
Male P	188.4	27.3	47			
Male R	176.0	21.8	27			
205–220:						
Male R	197.8	27.3	52	174.3	23.9	16
Female M ...	134.8	17.0	20	122.3	15.4	37
220–235:						
Male R	224.8	21.8	11	216.0	21.3	41
Female M ...	176.8	15.1	48	154.1	14.9	66
Female T ...	167.2	24.3	28			
235–250:						
Female T ...	198.0	16.7	39	187.9	13.5	32
250–265:						
Female T ...				203.1	18.8	40

Note. Each estimate is derived from the linear regression of daily δW (g · d^{-1}) on M (kJ · d^{-1}). Data sets were separated by individual (five birds), by W class and molt or nonmolt.

feather · wk^{-1}). For a W of 263 g, an energy equivalent of 19.5 J · mL O_2^{-1}, and a ratio of total feathers to flight feathers produced of 3:1 (from Wijnandts 1984, fig. 81), this slope reduces to 90 kJ · g^{-1}, a value even smaller than our measurements in the kestrel. Although admittedly an approximation, it suggests that feather synthesis in this carnivorous nonpasserine is also much less costly than synthesis in the three granivorous passerines. Thus there seems to be a main difference between small granivorous passerines and larger carnivorous nonpasserines (table 4). The former have higher absolute costs of feather synthesis (S), and, because energy deposited in the feathers (D) is not different (about 22 kJ · g^{-1}), the apparent efficiency (D/S) in the small passerines (about 6%) is lower than in the raptors (about 20%). This difference invites speculation about the underlying differences in physiology between the groups. There are at least two tentative explanations.

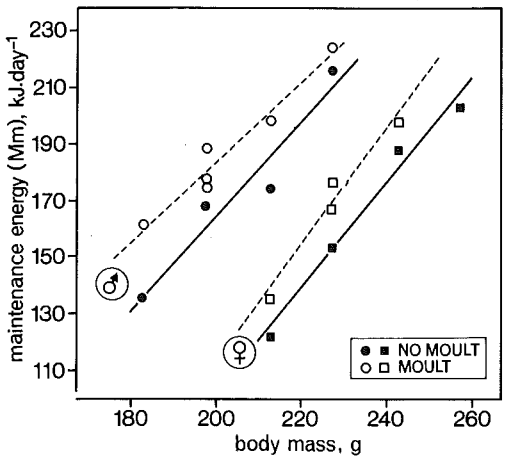

Fig. 6. Energy required for maintenance as a function of W for molting (open symbols) and nonmolting (solid symbols). Circles, males; squares, females. Lines were calculated by linear regression (see table 2).

First, carnivorous birds encounter higher protein concentrations in their diet than granivorous birds, and the energetic costs of feather synthesis may be dependent on the protein concentration in the food. In the white-crowned sparrow (*Zonotrichia leucophrys*) daily *M* during molt is independent of the sulfur-containing amino acid concentration of the diet (Murphy and King 1984*a*). These granivorous sparrows are typically able to meet the protein demands of feather synthesis through their normal food (Murphy and King 1984*b*), although they are unable to molt properly on a diet deficient in sulfur-amino acids (Murphy and King 1987). Yet the possibility is not excluded that the difference in the efficiency of feather synthesis between granivorous and carnivorous birds is rooted in their adaptation to different diets. For instance, protein degradation might be more efficient in carnivorous birds, but there is no positive evidence for such differences.

The second explanation for the observed difference in cost of feather synthesis between the raptors and small passerines is related to the low apparent efficiency of feather synthesis compared to synthesis of other tissues (Murphy and King 1984*a*). An explanation for this low efficiency is that the cost of feather synthesis is not primarily due to the synthesis of keratin itself, but to the production and maintenance of the tissues involved in feather production. Molt involves some major physiological modifications, such as changes in body composition (Dolnik and Gavrilov 1975, 1979; Chilgren 1977), increase in total blood volume (Chilgren and DeGraw 1977; DeGraw and Kern 1985), and increase in body temperature (Lustick 1970; Dolnik

TABLE 3

Regression of SMR on T_a below T_{lc} and BMR values during nonmolt (November–May), during the first part of molt (June–August), and during the last part of molt (September–October)

Bird and Season	SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$)	T_{lc} (°C)	BMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$)	Mean Mass ± SD (g)	Temperature Coefficient (W · $°C^{-1}$)	BMR (W)
Male R:						
Molt, first part	$2.13-.062 \cdot T_a$	17.7	1.03	192.7 ± 12.6	.065	1.08
	*		*			
Nonmolt	$1.54-.045 \cdot T_a$	16.7	.80	208.6 ± 12.0	.050	.90
			*			
Molt, second part ...	$1.63-.044 \cdot T_a$	16.5	.91	202.5 ± 8.0	.048	1.00
Female T:						
Molt, first part	$2.19-.064 \cdot T_a$	18.6	1.01	219.8 ± 9.5	.076	1.20
	*		*			
Nonmolt	$1.40-.039 \cdot T_a$	17.8	.71	237.4 ± 15.3	.050	.91
			*			
Molt, second part ...	$1.50-.033 \cdot T_a$	20.8	.81	233.9 ± 10.8	.041	1.03

Note. Asterisks indicate significant ($P < 0.05$, two-tailed Student *t*-test) differences between regression slopes or BMR values. Regression slopes and BMR were transformed to watts by multiplication with mean body mass and the energetic equivalent of O_2.

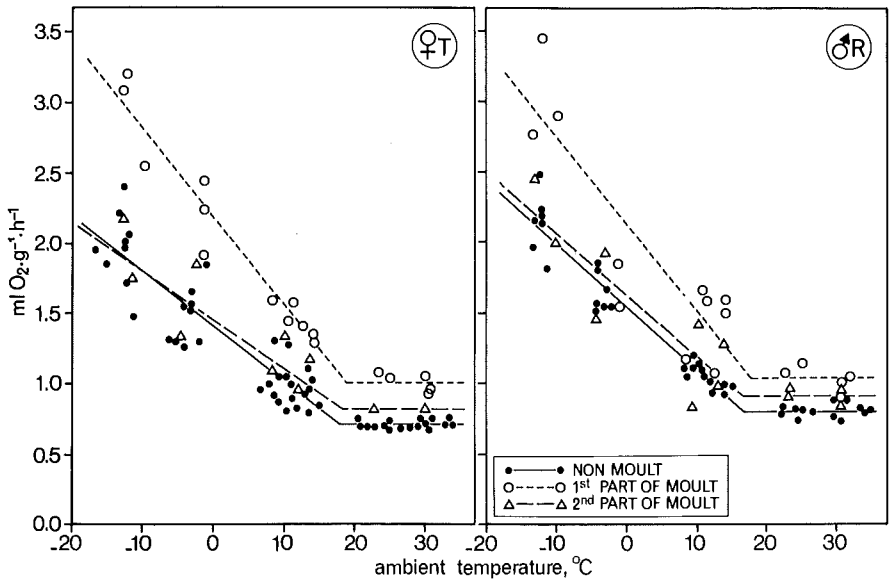

Fig. 7. Fasting metabolic rates (SMR) as a function of T_a *for female T and male R involved in Series II. Data were pooled for the first part of molt (open circles), the second part of molt (triangles), and the nonmolting period (solid dots). The regression of SMR on* T_a, T_{lc}, *and BMR were calculated by the hockey-stick routine (see text and table 3).*

and Gavrilov 1979; Wijnandts 1984; Newton 1986). Some of these occur already before the first feather is shed, as suggested by the increase in the temperature coefficient prior to molt onset (fig. 8). The energy costs involved in maintaining the keratin-forming tissues, increased blood volume, and higher temperature may be proportional not to feather mass formed but to general metabolic rate. If so, one would expect those costs to be lower in larger birds with a lower mass-specific BMR. Raptors and owls have basal and existence metabolic rates considerably below those of small passerines (Wijnandts 1984; Daan et al. 1989), partly as a consequence of their body size. A passerine of 25 g would have an existence metabolism of about 2.4 $kJ \cdot g^{-1} \cdot d^{-1}$ (Kendeigh, Dolnik, and Gavrilov 1977, figure 5.3), while a 210-g kestrel has an average M_m of about 0.8 $kJ \cdot g^{-1} \cdot d^{-1}$ (table 2). If molt-supporting tissues are proportional to W and require energy in proportion, they would account for a threefold difference in the synthesis cost of feathers between the passerines and the raptors. This corresponds roughly to the differences found (table 4).

If the second interpretation is correct, we would predict that the extra energy expenditure for feather synthesis ($kJ \cdot g^{-1}$) will be even smaller for

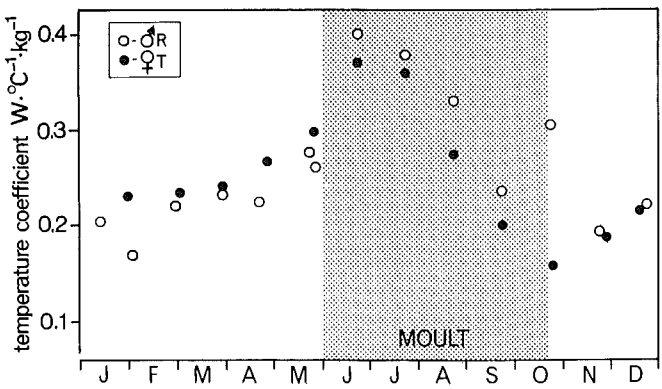

Fig. 8. Seasonal variation in the temperature coefficient of mass-specific SMR in two kestrels. Open circles, male R; solid circles, female T. The gray bar indicates the average molt period.

still larger birds such as geese. In contrast, the diet explanation would predict high energy costs for feather synthesis in these granivores. On the other hand, small carnivorous passerines would have a substantially reduced cost

TABLE 4
Summary of available estimates of S *exclusive of* D

Species	W (g)	$\dot{V}O_2$ Method S (kJ · g^{-1})	Source	Metabolizable Energy Method S (kJ · g^{-1})	Source
Fringilla coelebs . . .	20	230	1	397	1
Passer domesticus . .	27			416	2
Passer domesticus . .				835	3
Zonotrichia leucophrys	25	488	4	330	5
Falco tinnunculus	210	106	6	117	6
Asio otus	263	90	7		

Sources. 1, Dolnik and Gavrilov 1979; 2, Blackmore 1969; 3, Dolnik and Gavrilov 1975; 4, J. D. Chilgren, quoted in King 1981; 5, Murphy and King 1984*a*; 6, this study; 7, derived from Wijnandts 1984.

of molt according to the diet explanation, not according to the size explanation. Research is currently underway in our laboratory to evaluate these predictions.

Increased thermal conductance during molt has previously been demonstrated in other bird species (Lustick 1970; Thompson and Boag 1976; Dolnik and Gavrilov 1979; Wijnandts 1984). The increase has been attributed to the incomplete plumage cover, a decreased fat content of the body (Dolnik and Gavrilov 1975, 1979; Chilgren 1977), a larger blood volume related to the extension of the vascular system, especially in the pulp of the growing feathers (Chilgren and DeGraw 1977; DeGraw and Kern 1985), and to a slightly elevated body temperature during molt (Newton 1968; Lustick 1970; Dolnik and Gavrilov 1979; Wijnandts 1984). The increment in thermoregulatory requirements in the kestrel is considerable, especially during the first part of molt. Since the temperature coefficient already increased before the shedding of the first feathers, the incomplete plumage cover during molt is not the sole explanation. Some of the other physiological changes mentioned, such as increased skin vascularization, may have contributed to increased conductance. The consequences of molt for a bird's daily energy balance are probably largely due to an increased energy demand for thermoregulation, while the energy required for feather synthesis plays a minor role. The annual cycle in T_a in mid- and high-latitude regions must be important in the timing of molt in the annual cycle (Masman et al. 1988).

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